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Dispersal rates of Collembola in metal polluted soil

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Summary. Dispersal of soil animals may be affected by pollution. In this study the impact of heavy metals on dispersal rates of five collembolan species were estimated. The species differ in size, morphology and vertical distribution. Experiments were performed in plastic boxes filled with a 3 cm layer of mor soil with 1 cm of litter on top. The soils were sampled at one heavily copper and zinc polluted site and one unpolluted site with similar vegetation and soil. Approximately 55 animals were introduced at one end of each box. Three different experimental set-ups were used: 1) unpolluted soil; 2) polluted soil; 3) unpolluted soil with a "barrier" of polluted soil in the middle. Two boxes of each set-up were destructively sampled after 1, 2, 3 and 4 weeks. All tested Collembola species had a higher rate of dispersal in polluted than in unpolluted soil. Dispersal rates were correlated to mean adult body size of the species. The polluted barrier in unpolluted soil did not change dispersal rates or result in a distribution differing from that in unpolluted soil. More specimens were recovered after 2–4 weeks of incubation in unpolluted than in polluted soil. Dispersal tests using soil animals inhabiting the topmost layers of the soil, and thus exposed to anthropogenic activities, could be an alternative to soil toxicity tests focussing on sublethal effects on survival and reproduction, but have to be further elaborated.

Key words: *Isotoma notabilis*, *Isotomiella minor*, *Folsomia quadrioculata*, *Onychiurus armatus*, *Tullbergia* spp., dispersal, Collembola, soil

Introduction

Dispersal, i. e. the spreading out of a population from one site to one or several others, is important to demographic and evolutionary dynamics of populations (Levin 1995). It may lead to aggregation at sites (patches) suitable for reproduction and feeding or to a spacing out of individuals competing for resources. In an environment where patch quality varies in space and time the ability to traverse less suitable patches and find acceptable ones is crucial for the survival of a population. Dispersal rate and ability to endure stress determine how far apart suitable patches can be and still allow a population to exist.
Dispersal rates of soil-living Collembola are largely unknown. In two microcosm experiments similar values of mean dispersal rate were found for *Onychiurus armatus* (Tullberg) (1.4 and 1.9 cm day^{-1}) (Sjögren et al. 1994; Bengtsson et al. 1994). A few cases of dispersal in surface-living species have been described: directional movement over snow (Hågvar 1995), swarming on the snow surface in response to increased temperature (Leinaas 1981, 1983a), and circatidal movements in response to high and low tides (Joosse 1966; Foster &

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Moreton 1981). No studies of natural movements of Collembola through a three-dimensional mor soil have been reported.

Optimal foraging models predict that when food supply is depleted and the rate of food gain decreases an animal will eventually do better if it leaves its present location than if it stays (Pyke 1984). At low population densities of soil Collembola such a food related probability of leaving a patch has been shown (Bengtsson et al. 1994). Metal deposition affects the soil habitat both by reducing the densities of fungal hyphae, an important food resource for many collembolan species (Vegter 1982; Takeda & Ichimura 1983; Hasegawa & Takeda 1995), and by changing the abundances of preferred fungal species (Nordgren et al. 1983; Bengtsson et al. 1985), thus altering a suitable habitat into a less suitable one. Physical soil properties are also affected. Hence, waterholding capacity is reduced (Sjögren et al. 1995), which may increase the mortality of drought sensitive animals. An accumulation of slowly decomposing organic matter at polluted sites also changes the structure of the soil habitat, presumably modifying the size distribution of pores through which the animals move.

The purpose of this work was to test if collembolan dispersal rate will be higher in a metal polluted soil than in an unpolluted one. The generality of the response to metal pollution was tested by using five species representing a range of sizes, morphologies, and preferences as to soil depth. The effect on dispersal rate of a barrier of polluted soil between two patches of unpolluted, simulating a patchy soil environment, was also tested.

Materials and Methods

Mor and litter soils were collected at two mature coniferous forest sites NW of a brass mill near Gusum, SE Sweden (sites II and V in Bengtsson & Rundgren (1988)). The soils were sieved (mor < 5.7 mm, litter > 5.7 mm), frozen (–18 °C) and thawed three times to reduce indigenous invertebrate fauna. Unpolluted mor soil (site V) contained 43 mg Cu + Zn kg^{-1} d. wt soil and polluted mor soil (site II) 1683 mg Cu + Zn kg^{-1} d. wt soil. Unpolluted and polluted litter contained 238 and 20048 mg Cu + Zn kg^{-1} d. wt soil, respectively (Bengtsson & Rundgren 1984, 1988).

Dispersal experiments were performed using plastic boxes (24 × 11 × 7 cm) with a 0.5 cm bottom layer of plaster of Paris moistened with tap water to keep soil moisture conditions constant. The plaster bottom was covered with a 3 cm thick layer of mor, which had a 1 cm thick layer of litter on top. Three different experimental set-ups were used: unpolluted and polluted soil along the whole length of the box, and 8 cm of unpolluted soil at each end of the box with an 8 cm "barrier" of polluted soil in between (Fig. 1).

Five of the most common species of Collembola in soil from the unpolluted site (V) (Bengtsson & Rundgren 1988) were used for the experiments: *Folsomia quadrioculata* (Tullberg), *Isotoma notabilis* (Schäffer), *Isotomiella minor* (Schäffer), *Onychiurus armatus* (Tullberg) and *Tullbergia* spp. They were extracted in a modified high-gradient extractor (Macfadyen 1961). The species above are listed in

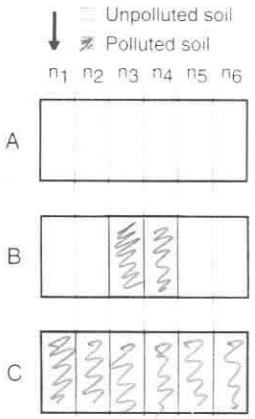

Fig. 1. Experimental boxes with unpolluted soil (A), a polluted "barrier" in unpolluted soil (B) and with polluted soil (C). The Collembola were introduced in the middle of strip n_1 indicated by an arrow. After incubation specimens were extracted from 6 strips of soil: n_1–n_6. The polluted soil was collected in close vicinity of the brass mill at Gusum, SE Sweden

decreasing order with the largest and most superficially found species first and the smallest with a preference for deeper soil layers last (Fjellberg 1980; Hågvar 1983).

To minimize handling approximately 55 adult Collembola were transferred directly from the extraction apparatus to an area (4 × 11 cm) at one end of each box (n_1 in Fig. 1). The number of individuals of a species varied between boxes, due to the outcome of the extraction. The initial density of a box (12 500 ind. m^{-2}) was close to the mean density (17 300 ind. m^{-2}) at two unpolluted sites in the Gusum area (Bengtsson & Rundgren 1988).

A lid was put on each box to reduce evaporation and prevent Collembola from escaping. Air could pass through two holes (diameter 4 cm) in the lid, each covered with a net (mesh 3 mm). To correct for evaporation, the boxes were weighed once a week and distilled water was added if needed. The boxes were incubated for 1, 2, 3 or 4 weeks at 16 °C and in darkness (n = 2 for each set-up and incubation time). The temperature represents summer conditions in the south of Sweden.

The boxes were destructively sampled after incubation. The soil was lifted out of the boxes in 4 cm wide "strips" with a putty knife (n_1–n_6 in Fig. 1). Collembola were extracted separately from each of the six strips using the high gradient extractor, identified to species, developmental stage (adult or juvenile) and counted.

Mean dispersal distance (D) for the individuals of each species was calculated as

$$D = \Sigma n_i d_i / \Sigma n_i$$

where d_i is the distance between the site of introduction and the strip i, in which the animals were found and n_i is the number of animals found in strip i.

Differences in recovery and distribution of Collembola between set-ups were analysed in pairwise contingency tables for each incubation time. Dispersal distances were compared using the non-parametric Kruskal-Wallis test.

Results

The numbers of Collembola recovered from polluted soil decreased with incubation time ($X_{poll}^2 = 9.425$, $p = 0.0241$), while numbers increased in the unpolluted and barrier set-ups ($X_{unpoll}^2 = 25.429$, $p = 0.0001$, $X_{barr}^2 = 9.873$, $p = 0.0197$) (Table 1). *O. armatus* and *F. quadrioculata* had the highest mean recoveries, 64 and 78 %, while *Tullbergia* spp. had the lowest, 33 %. The results probably reflect a difference in extraction efficiency of the species and differential mortality. After 4 weeks of incubation *I. notabilis*, *O. armatus* and *F. quadrioculata* had reproduced in the unpolluted soil (34 juveniles) while only 5 juvenile *O. armatus* were found in the polluted soil. No juveniles were found in the barrier set-up.

Collembola (all species) in polluted soil had travelled further than those in unpolluted soil as seen from the difference in mean dispersal distances in the two soils independent of incubation time (Fig. 2, Table 2). The distributions of all individuals in unpolluted soil with a polluted barrier and the unpolluted soil were similar. *F. quadrioculata*, *O. armatus* and *I. minor* were recovered in sufficient numbers to test for differences between their distributions in dif-

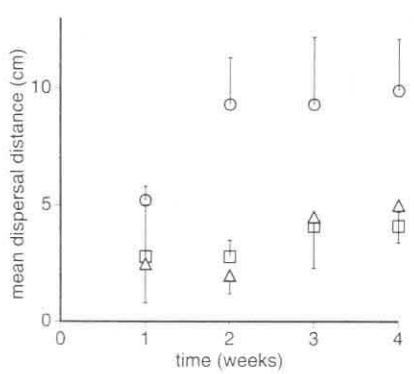

Fig 2. Mean dispersal distance of all Collembola after 1–4 weeks of incubation in unpolluted (□), polluted (○) and unpolluted soil with a polluted barrier (△) (n = 2). Mean and SD are given

Table 1. Numbers of recovered test animals from dispersal experiments in each of the two replicates. Collembola recovered after four weeks of incubation were separated into adults and newly hatched juveniles. The numbers of added specimens are given within parenthesis

Unpolluted soil	*Incubation time (weeks)*				
	1	**2**	**3**	**4**	
				adults	*juveniles*
All Collembola	14, 26 (55, 56)	37, 35 (56, 55)	41, 31 (55, 55)	26, 36 (55, 55)	16, 19
Folsomia quadrioculata	5, 6 (12, 8)	13, 13 (14, 16)	16, 9 (17, 11)	9, 12 (10, 12)	0, 3
Isotoma notabilis	2, 0 (5, 1)	2, 0 (5, 3)	5, 1 (5, 5)	3, 6 (3, 6)	7, 14
Isotomiella minor	2, 4 (7, 13)	10, 6 (18, 14)	9, 9 (16, 16)	4, 3 (9, 10)	0, 0
Onychiurus armatus	3, 14 (17, 25)	10, 14 (13, 15)	10, 11 (14, 15)	10, 14 (21, 22)	9, 2
Tullbergia spp.	2, 2 (14, 9)	2, 2 (6, 7)	1, 1 (3, 8)	0, 1 (12, 5)	0, 0
Polluted soil	*Incubation time (weeks)*				
	1	**2**	**3**	**4**	
				adults	*juveniles*
All Collembola	30, 32 (57, 55)	24, 33 (55, 55)	21, 19 (55, 55)	24, 25 (55, 55)	4, 1
Folsomia quadrioculata	12, 10 (17, 11)	13, 9 (15, 16)	7, 10 (10, 15)	4, 11 (9, 16)	0, 0
Isotoma notabilis	3, 4 (3, 7)	0, 2 (3, 2)	0, 0 (3, 3)	8, 0 (8, 2)	0, 0
Isotomiella minor	3, 3 (11, 9)	5, 8 (18, 12)	2, 1 (12, 13)	3, 1 (12, 9)	0, 0
Onychiurus armatus	10, 11 (15, 15)	6, 12 (15, 20)	11, 8 (22, 20)	9, 10 (14, 14)	4, 1
Tullbergia spp.	2, 4 (11, 13)	0, 2 (4, 5)	1, 0 (8, 4)	0, 3 (12, 14)	0, 0
"Barrier"	*Incubation time (weeks)*				
	1	**2**	**3**	**4**	
				adults	*juveniles*
All Collembola	27, 37 (55, 56)	37, 39 (58, 56)	39, 37 (55, 53)	41, 48 (55, 61)	0, 0
Folsomia quadrioculata	0, 0 (0, 0)	0, 0 (0, 0)	0, 0 (0, 0)	1, 1 (1, 1)	0, 0
Isotoma notabilis	5, 0 (6, 2)	0, 3 (1, 5)	0, 1 (1, 1)	0, 0 (0, 0)	0, 0
Isotomiella minor	13, 19 (31, 26)	18, 12 (28, 19)	13, 14 (17, 25)	16, 18 (16, 23)	0, 0
Onychiurus armatus	8, 18 (15, 28)	6, 22 (24, 27)	25, 22 (36, 27)	23, 24 (35, 32)	0, 0
Tullbergia spp.	1, 0 (3, 0)	3, 2 (5, 5)	1, 0 (1, 0)	1, 5 (3, 5)	0, 0

Table 2. Mean distance (cm), D. travelled by recovered adult Collembola in the dispersal experiment (n = 2). An even distribution of specimens over the box would give a mean dispersal distance of 10.0 ± 6.8 cm. Differences in distribution of dispersal distances between the three set-ups (unpolluted, polluted, polluted barrier) were tested with contingency table analysis

All species				
	Incubation time (weeks)			
	1	**2**	**2**	**4**
Unpolluted soil	2.8 ± 2.2	2.8 ± 0.7	4.1 ± 0.5	4.1 ± 0.6
Polluted soil	5.2 ± 0.6	9.3 ± 2.0	9.3 ± 2.9	9.9 ± 2.2
Polluted barrier	2.5 ± 1.7	2.0 ± 0.8	4.5 ± 2.2	5.0 ± 1.6
X^2	19.789	65.033	42.634	35.299
p	0.0313	0.0001	0.0001	0.0001
Folsomia quadrioculata				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	6.1 ± 4.9	4.9 ± 1.3	5.7 ± 1.8	7.0 ± 1.1
Polluted soil	9.3 ± 2.7	12.2 ± 1.5	8.7 ± 2.2	10.2 ± 1.1
Polluted barrier	–	–	–	18.0 ± 2.8
X^2	9.17	15.169	4.355	11.683
p	0.1025	0.0097	0.4995	0.3068
Isotomiella minor				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	2.0 ± 0.0	1.7 ± 1.3	2.7 ± 1.3	4.3 ± 2.4
Polluted soil	3.3 ± 4.7	7.2 ± 4.5	13.0 ± 9.9	9.3 ± 1.9
Polluted barrier	2.0 ± 0.7	2.4 ± 0.9	3.4 ± 1.2	4.7 ± 0.4
X^2	5.744	12.467	21.537	13.821
p	0.6758	0.0523	0.0176	0.1813
Onychiurus armatus				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	1.6 ± 1.5	1.9 ± 2.1	4.2 ± 0.8	2.7 ± 1.8
Polluted soil	3.2 ± 1.1	7.3 ± 2.8	10.7 ± 6.8	8.2 ± 0.9
Polluted barrier	2.6 ± 2.0	1.8 ± 0.8	5.2 ± 2.7	5.1 ± 2.1
X^2	6.319	35.103	26.087	13.271
p	0.6116	0.0001	0.0036	0.2089

ferent soils. They had all travelled further in polluted than in unpolluted soil after 2 weeks. A longer incubation time, >2 weeks (*F. quadrioculata*) and 4 weeks (*O. armatus, I. minor*), reduced the difference between set-ups since the animals reached the end of the box and thus spread out evenly in the soil.

Mean dispersal rates of all species during the first week of incubation were 0.4 (unpolluted soil) and 0.7 cm day^{-1} (polluted soil) (Table 3). The species varied in dispersal rate with *F. quadrioculata* being the fastest both in unpolluted (0.9 cm day^{-1}) and polluted soil (1.3 cm day^{-1}). *I. minor* had a dispersal rate of 0.3 and 0.5 cm day^{-1}, respectively, and *O. armatus* 0.2 and 0.5 cm day^{-1}. The estimated dispersal rates were generally lower when calculated from

Table 3. Mean dispersal rates (cm day $^{-1}$) of recovered adult Collembola in the dispersal experiment (n = 2)

All species				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	0.4	0.2	0.2	0.1
Polluted soil	0.7	0.7	0.4	0.4
Polluted barrier	0.4	0.1	0.2	0.2
Onychiurus armatus				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	0.2	0.1	0.2	0.1
Polluted soil	0.5	0.5	0.5	0.3
Polluted barrier	0.4	0.1	0.2	0.2
Folsomia quadrioculata				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	0.9	0.4	0.3	0.2
Polluted soil	1.3	0.9	0.4	0.4
Polluted barrier	–	–	–	0.6
Isotomiella minor				
	Incubation time (weeks)			
	1	**2**	**3**	**4**
Unpolluted soil	0.3	0.1	0.1	0.2
Polluted soil	0.5	0.5	0.6	0.3
Polluted barrier	0.3	0.2	0.2	0.2

the distribution of dispersal distances after 2 weeks of incubation. This indicates a high initial dispersal rate probably due to handling or population density.

There was a significant positive correlation between Collembola size and dispersal rate both in unpolluted (correlation coefficient: 0.880, r = 0.880, $p < 0.05$) and polluted soil (correlation coefficient: 0.891, r = 0.891, $p < 0.05$) (Fig. 3).

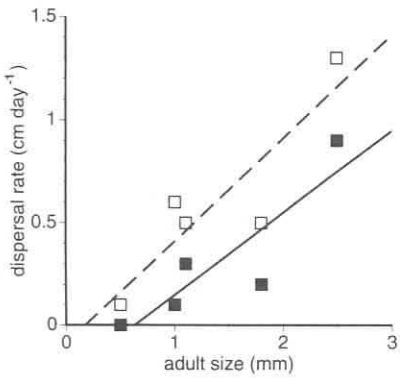

Fig. 3. Regression of species specific dispersal rate (Table 4) on adult size of Collembola in unpolluted (■) ($R^2 = 0.775$, p = 0.049) and polluted (□) soil ($R^2 = 0.793$, p = 0.043)

Discussion

A mean dispersal rate of 0.2 cm day^{-1} for the Collembola species implies that a population, i.e. individuals released at one point, would be able to spread over 1.7 m^2 in a year. This is probably an overestimation because of inactivity during moulting (Leinaas 1983b). Lower activity during months with soil temperatures less than 16 °C (experimental conditions) should also be expected. Adult size of a species explained 78 % of the variation in dispersal rate (Fig. 3), which suggests that movement is age dependent. The three species with furca, *I. notabilis*, *I. minor* and *F. quadrioculata*, did not move faster than would be predicted from their size. This implies that ability to jump does not further increase dispersal rate.

An increase in dispersal rate seems to be the general reaction to low habitat quality (here: high metal concentrations). This should enable some individuals to find a suitable habitat faster than if they were to disperse at the same rate as in unpolluted soil. As the number of survivors decreases with time spent in polluted soil there must be a time limit to search for better conditions. A high dispersal rate can thus help to maintain populations in an environment consisting of acceptable patches in an unhospitable soil matrix.

A minor barrier of polluted soil did not restrain any of the tested species from leaving the part of the box where they were released. Likely, a patchy environment at a 10 cm scale does not restrain these species from finding suitable patches, except maybe for *Tullbergia* spp. which is bound to deeper layers and has a very low dispersal rate. Distances of several metres between suitable patches may prevent or at least detain colonization by collembolan populations bound to the deep soil layers. The importance of phoresy and aerial dispersal of soil-living Collembola for colonization rate of suitable patches and gene flow between populations still remains to be investigated.

The five tested species are common at unpolluted sites in a gradient of metal pollution around the brass mill of Gusum and all except *F. quadrioculata* are also found at the most polluted sites although at low densities (Bengtsson & Rundgren 1988). The large variation in metal content between 10 cm^2 soil samples at the polluted sites (Bengtsson & Rundgren 1988) suggests the existence of high quality patches (= low metal concentrations), which could serve as refuges for soil animals. In combination with physiological or behavioural adaptations to high soil metal concentrations (Tranvik et al. 1993, 1994) an ability to move between acceptable patches may explain the persistence of populations at the highly polluted sites.

Dispersal rate could be a suitable parameter in toxicity testing in which sublethal effects of pollutants are assessed. The generality of the response, the short duration of incubation and the relative easiness with which at least some of the tested collembolan species are kept in laboratory cultures are factors in favour of such a test system. The sensitivity of dispersal rate to low concentrations of pollutants remains to be shown.

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